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THE NEW ENGLAND BOTANICAL CLUB

Vol. 57 July, 1955 No. 679

DISTRIBUTION AND ABUNDANCE OF SHORTIA GALACIFOLIA

P. A. Davies

From 1839, when Asa Gray found an unnamed specimen from the Carolinas in André Michaux's herbarium in Paris and named it *Shortia galacifolia*,[1] until 1877 when George M. Hyams rediscovered a small station of it on a hillside near a small stream which flowed into the Catawba River about five miles north of Marion in McDowell County, North Carolina,[2] the prime efforts of botanists and collectors was its rediscovery. Following Hyams rediscovery of *Shortia*, the effort shifted to determining its distribution and abundance. In 1879, Asa Gray and party, including Charles S. Sargent of the Arnold Arboretum, sought for additional plots without success on the west side of the Linville Mountains at North Cove and on the Iron Mountain Range, both in the region of Hyams' discovery.[3] No more extensive excursions or discoveries were made in this area until recently.

Nine years after Hyams' discovery, Charles S. Sargent, with his guide, Frank E. Boynton of Highlands, North Carolina, while seeking Michaux's *Magnolia cordata* at the headwater of the Keowee River, found *Shortia galacifolia* near the confluence of the Horsepasture and Toxaway Rivers in Oconee County, South Carolina.[4] Desiring additional specimens and information on its distribution and abundance, Sargent requested

[1] Gray, Asa, Amer. Jour. Sci. & Arts 42: 48, 1842.
[2] Letter, J. W., Congdon to Asa Gray, Oct. 18, 1878 (Gray Herb.).
[3] Redfield, J. H., Bull. Torrey Bot. Club 6: 331–336, 1879.
[4] Sargent, C. S., Amer. Jour. Sci. & Arts, Ser. III, 32: 466–473, 1886.

Boynton to return to the forks of the river, their collecting ground of the previous month, and explore the region. This Boynton did and found large quantities of *Shortia* on Bearcamp Creek, a lower tributary of the Horsepasture River.[5] Three years later (1889) Boynton found acres of it in the locale of the junction of the Whitewater River and Devilfork Creek and in the lower Jocassee Valley, all in Oconee County, South Carolina.[6] In the spring of 1890, T. G. Harbison found *Shortia* in great abundance on the Horsepasture River between its junction with the Toxaway River and Bearcamp Creek.[7]

The acres of *Shortia* that F. E. Boynton discovered along the Whitewater River in Jocassee Valley were easily accessible by roads and trails. Now that an abundant supply had been found, more than enough to meet the demands of botanists for herbarium specimens and nurserymen to supply the public with living plants, the scientific interest brought on by nearly fifty years of intensive search for it was lessened. Almost an equal amount of time was to pass before interest was again awakened for additional knowledge on its distribution and abundance.

Charles F. Jenkins sought information on the distribution of *Shortia* by assembling data from herbarium sheets in thirty-one of the leading herbaria in the United States. In all he found ninety-eight sheets and gave the distribution as follows: "Forty-four were collected along the banks of the Whitewater River in Oconee County, South Carolina. Fourteen more are listed as coming from the Jocassee Valley, also in Oconee County. Thirteen were found in McDowell County, North Carolina, more definite locations not being given. Eight were found in the Toxaway Gorge in Transylvania County, North Carolina, three along Bearcamp Creek and two along the Horsepasture River, both located in Transylvania County. One each from the mountains of N. W. Carolina, four miles N. W. Salem, South Carolina, and Macon County, North Carolina. The remainder are specimens with labels giving no definite locality or coming from cultivated plants."[8]

[5] Letter, F. E. Boynton to C. S. Sargent, Nov. 7, 1886 (Gray Herb.).
[6] Boynton, F. E., Garden & Forest, 2: 214–215, 1889.
[7] Clute, W. N., Amer. Bot. 32: 65–68, 1926.
[8] Jenkins, C. F., Arnoldia 2: 13–28, 1942.

In the library of the Botany Department, University of North Carolina, is a distributional map of *Shortia* prepared by William C. Coker from both herbarium sheets and field records. For McDowell County, North Carolina, he gives stations on Tom's Creek, branches of John's Creek, and several places on the east side of the lower part of Bald Mountain. Dr. Coker includes on his map the single station reported by F. M. Crayton on the Linville River west of Table Rock Mountain in Burke County, North Carolina. On the Keowee River and its sources in Pickins County, South Carolina, he lists two locations on the east side of the Keowee River below the entrance of Big Eastatoe Creek; in Oconee County, South Carolina, four stations above the entrance of Big Eastatoe Creek, sixteen places on the upper sources of Little River, and several plots along the Whitewater; and in Transylvania County North Carolina, three records along the Toxaway River and two on Toxaway Creek.[9]

The southernmost location is the one discovered by A. B. Massey in 1911 on the Keowee River below the entrance of Little River. In recording his discovery Massey relates, "This is a small station on the bank of the Keowee River at the foot of a wooded bluff. When I last visited the place, there were only a few plants; however, it may have increased in recent years."[10] On November 3, 1952, D. E. Wade visited Massey's station and explored the area adjacent to it. He describes his observations: "In a rocky ravine there are at least six clumps of *Shortia*, the largest [Massey station] was approximately 3 by 6 feet at an elevation of about 615 feet, while the highest was at about 680 feet. The entire ravine is cooled by a small stream which is fed by springs at various places. The woody plant life is marked by hemlock, rhododendron, laurel, holly and beech. It looks as if the stand had been there many hundreds of years. Most of the clumps are definitely above flood level."[11] In July 1953, D. C. Wade showed the writer the Massey station and the additional stands he found. The clumps were restricted and the plants were rather small but healthy.

[9] Map, W. C. Coker, Botany Dept. University of North Carolina, copy sent to P. A. Davies, May 18, 1948.

[10] Map, A. B. Massey to P. A. Davies, June 30, 1952.

[11] Map and letter, D. E. Wade to P. A. Davies, Nov. 7, 1952.

C. F. Moore of Brevard, North Carolina, located several stands on the Keowee River between Laurel Branch and Whitewater River, a single station near the source of Laurel Branch, a small area on the Bearwallow Creek about one-half mile from its mouth, and on subsequent visits with B. C. Olney observed many patches along the lower part of this creek. They also found *Shortia* on Rock House Creek, near the mouth of Laurel Fork Creek, on the Keowee River between Laurel Branch and the Toxaway River, along the Whitewater River in Jocassee Valley, on eastern branches of the Horsepasture River and along a ridge between the Horsepasture River and Bearwallow Creek.[12]

In April, 1917, W. W. Diehl saw *Shortia* in abundance and in full bloom on the northeast bank of the Whitewater River between the Thompson and Toxaway Rivers, and on three other occasions between 1921 and 1927 near the mouth of Bearwallow Creek.[13] In the Gray Herbarium is a specimen collected by E. T. Wherry on July 12, 1936 along Bearwallow Creek and another by H. J. Oosting on July 15, 1936 in the Toxaway Gorge, Transylvania County, North Carolina. During March, 1944, A. E. Prince, J. A. Berly and O. L. Cartwright found *Shortia* in flower along the road near the Whitewater River just below the entrance of Devilfork Creek and later (1946) Prince found it plentiful on the right bank of the Toxaway River above its confluence with the Whitewater River.[14] The Rev. A. Rufus Morgan, Franklin, North Carolina, found *Shortia* on the Toxaway River above the North Carolina border and on the Whitewater River just above its junction with the Thompson River.[15] W. H. Duncan reported a station in an open woods along a tributary of Middle Fork Creek in Oconee County, South Carolina.[16]

In March 1949, W. H. Duncan, Haskell Venard and G. W. McDowell discovered the first station in Georgia. It was a small colony (8 × 4 feet) near Reed Creek in Rabun County, and in August of the same year Duncan found a smaller colony near the original one.[17]

[12] Map, C. F. Moore to P. A. Davies, June 30, 1952. Also, letter, Aug. 2, 1954.
[13] Letter, W. W. Diehl to P. A. Davies, Sept. 23, 1952.
[14] Prince, A. E., Rhodora, 49: 159–161, 1947. Also, map and letter, May 24, 1953.
[15] Map, A. Rufus Morgan to P. A. Davies, Aug. 8, 1951.
[16] Letter, W. H. Duncan to P. A. Davies, May 23, 1952.

Several healthy and expanding patches of *Shortia* are present in Highlands, North Carolina and its environs. All available data indicate that these plantings were made from plants gathered by F. E. Boynton, T. G. Harbison and others along the sources of the Keowee River, particularly the Whitewater River. The writer has examined many streams and their smaller tributaries about Highlands that appear to offer suitable habitat without finding a single indication of *Shortia.*

Many sources of reference state that *Shortia galacifolia* is rare. These statements have probably arisen from the fact that Asa Gray and his colleagues sought for it without success for thirty-eight years (1839–1877) and the patch that G. M. Hyams finally discovered near a tributary of the Catawba River was too small to supply the demands for herbarium specimens. The recently discovered patches along the sources of this river are not numerous. On the sources of the Keowee River most collectors have observed *Shortia* on the fringe of its range or have made distributional judgments from the colonies within easy reach by roads or trails along the Whitewater River or Bearwallow Creek. In certain places on the drainage areas of the Toxaway and Horsepasture Rivers it is one of the most abundant plants, and F. E. Boynton, C. F. Moore, B. C. Olney, and the writer have observed patches containing one or more acres. Until recently the areas containing an abundance of *Shortia* on the sources of the Toxaway and Horsepasture Rivers were accessible only by a few strenuous trails and nonserviceable roads. Over the Poinsett Lumber and Manufacturing Co. road to these areas, *Shortia* may now be seen in abundance.

Shortia grows in various habitats: hanging from rocks near water falls (water dripping from its leaves) in sand at the edge of running water, on fallen decaying tree-trunks, in shady, deep, moist loam soils, and on dry hillsides. Its most favorable habitat is a cool, damp, shady stream bank, with moist circulating air, and a surface covering of two to six inches of loose organic debris with a fertile, moderately acid soil (pH 4.2–6.0) beneath. While *Shortia* is more frequently found beneath *Rhododendron maximum* it will grow equally as well under the shade of *Tsuga*

[17] Duncan, W. H., Haskell Venard and G. W. McDowell, Rhodora 52: 229–232, 1950.

canadensis, Pinus Strobus, Pinus rigida, Liquidambar Styraciflua, Liriodendron Tulipifera and other acid tolerating trees and shrubs. Plants found in the most favorable habitats have large leaves with long petioles and large flowers on long peduncles; while those growing under less favorable conditions (dry hillsides) have smaller leaves on short petioles and small flowers on shorter peduncles.

Fortunately for the preservation of *Shortia*, the largest percentage of it is confined to large private holdings and government land. Along the Toxaway and Horsepasture Rivers and their tributaries in Oconee and Pickens Counties, South Carolina, the Poinsett Lumber and Mfg. Co. holds the areas of greatest concentration of *Shortia*, while in Transylvania County, North Carolina, it is the Duke Power Co. which controls such areas. The writer, his colleagues and students are indebted to Thomas Mitchell and Furman Chastain of the Poinsett Lumber and Mfg. Co. and C. F. Moore of the Duke Power Co. for permission to seek *Shortia* on the company lands. On the sources of the Catawba River in McDowell County, North Carolina more than one-half the *Shortia* plants are in the Pisgah National Forest. Both the public and private organizations have the means of controlling the destroyers of it, so *Shortia* is safe for posterity.

The writer became interested in *Shortia* while preparing a paper on the life of Charles W. Short, first of the Kentucky born botanists and recipient of Asa Gray's honor, for the Filson Club History Quarterly.[18] Available references on *Shortia* did not present a unified picture of its distribution and little could be found about its abundance. In order to obtain more complete knowledge of its distribution and abundance, investigations were made which included extensive field excursions and the following of all significant leads through correspondence and conversations with persons who had collected *Shortia* or had heard of places where it could be found.

Explorations were made by working up or down the rivers, creeks, or branches. Not all the small tributaries were followed to their sources. In several places the terrain was too rough or the thickets so impenetrable that no explorations were made

[18] Davies, P. A., Filson Club Hist. Quart., 19: 131–155, and 19: 208–249, 1945.

for fear of bodily injuries. Most of the surveys were made in dry weather and at low water stages, so the explorers were able to wade the streams through most of the gorges and to escape the dense thickets.

It was the author's original intention to publish a full account of the distribution of *Shortia*, giving exact plot locations. Realizing that unscrupulous collectors might destroy the easily accessible small patches, particularly on the fringes of the range, he decided to publish only general locations, and to deposit in the library of the Gray Herbarium data on exact location, including maps, and the correspondence accumulated during the study. In this way *Shortia* may be protected and the information on exact locations be made available to anyone interested in checking various plots or continuing the study of its distribution.

The most southern extensive search by the writer and his colleagues was on the middle and eastern sources of Little River near the divide which separates its watershed from that of the Whitewater River. Along these small headwater streams many scattered patches were observed. A more complete survey of the smaller western branches would undoubtedly yield many new locations.

Jocassee Valley, located in Oconee County, South Carolina, extends from above the confluence of the Whitewater and Thompson Rivers to below the Chapman Bridge over the Keowee River. Many streams enter the valley. The largest are the Whitewater, Thompson and Toxaway Rivers and Devilfork Creek. The writer has carefully examined all parts of the valley. The acres of *Shortia* that Boynton discovered in 1889 have largely been destroyed by cultivation, grazing and road building. However, along many of the streams and on some of the steeper slopes where grazing has not taken place, *Shortia* is still plentiful. There is enough of it in the valley to meet the demands of nurserymen for hundreds of years. The author knows of one ravine near the Keowee River where nurserymen have been gathering *Shortia* for more than 30 years without greatly depleting it.

At the upper end of the valley, along the camp road on the south side of the Whitewater River, a few colonies of *Shortia* were observed. This river was explored all the way to the

upper falls and no *Shortia* was found beyond the first road-bridge (elevation circa 1060 feet) above its confluence with the Thompson River.

Following the Thompson River from its junction with the Whitewater to approximately the North Carolina boundary numerous patches of *Shortia* were observed. This river was again examined above state highway 92 (Upper Whitewater Falls Road) without finding any indication of *Shortia*. Wright and Coley creeks, the two main eastern tributaries of the Thompson River in South Carolina were examined to their sources. As the elevation increased, *Shortia* became more abundant. Near the divide which separates the branches of Coley Creek from those of Mill Creek, the writer found on the Coley Creek side, a patch of *Shortia* on a moist, steep and shaded hillside. Below and near the patch were numerous young plants which were judged to be from one to three years old. In 1953, C. F. Moore and the writer found a similar condition below a patch and near the edge of Bearwallow Creek. This is a clear and encouraging indication that in certain places where conditions are favorable, *Shortia* is increasing rather than decreasing. No attempt was made to explore the tributaries of the Thompson River between the North Carolina boundary and state highway 92.

On Devilfork Creek, the large southern tributary of the Whitewater River, scattered stations were recorded along its banks, but many were present higher up on the mountain along the numerous branches of the lower tributaries. As the headwaters of the southern branches of this creek are separated by narrow ridges from the northern branches of Little River, the upper stations on each drainage area are in close proximity.

The Toxaway River ends in Jocassee Valley by joining the Whitewater to form the Keowee River and extends northward into its numerous branches above the old Lake Toxaway site in Transylvania County, North Carolina. Along its course many streams flow into it, but the majority are small and unnamed. On its banks and along its numerous tributaries *Shortia* is plentiful, some in small isolated patches, others in large areas extending up the mountainside. No *Shortia* was found one fourth mile above the entrance of Bearwallow Creek, although

the river was examined into its sources. Only the larger creeks and branches of the Toxaway River which appear on topographic maps will be considered in this paper although a great many of the smaller branches contain an abundance of it.

The center of distribution of *Shortia* for the sources of the Keowee River basin appears to be along the Toxaway River below the entrance of Horsepasture (Green) River and near that of the Devil's Hole Creek. This position is approximately halfway between the stations to the south on the northern branches of Little River, along Devilfork Creek, on the Whitewater River and those to the north on Bearwallow Creek. In an east-west direction it is between the station on the upper part of Laurel Fork Creek and the Thompson River. It is interesting correlation that it was near this center of distribution, at the forks of the Toxaway and Horsepasture Rivers, that C. S. Sargent believed André Michaux, in the inclement weather of December 1788, collected the type specimen and that he almost a hundred years later (September, 1886) rediscovered it for this part of the Carolinas.

Several large and many small streams enter the Toxaway River from its junction with the Whitewater to the south and the Horsepasture to the north. All except Devils Hole Creek are unnamed and *Shortia* was found, varying in abundance, on nearly all of them. As one passes through the Toxaway watershed over the Poinsett Lumber and Mfg. Co.'s new road to the confluence of the Toxaway and Horsepasture Rivers, *Shortia* may be observed in abundance along the branches of Devil's Hole Creek and other streams in this area. Because of the recent cutting of trees along the upper branches, resulting in the drying of the surface debris, and the covering of the leaves with dust from the dirt road, a large part of these stands may not survive.

On the Horsepasture River between its junction with the Toxaway and Bearcamp Creek (main tributary of the Horsepasture in South Carolina), the great amount of *Shortia* that T. G. Harbison observed in 1890 was still there when the area was examined in March of 1951 by the author accompanied by L. M. Brown, and in June of the same year with Arland Hotchkiss. Both sides of the river were checked and the larger

amount was found on the more gently, less exposed, southwestern slopes. Rocks and soil dumped on the lower side of a new logging road built around the mountain in the latter part of 1951 buried many large patches. Above the road *Shortia* can still be found in considerable quantities.

Along the Horsepasture River above the entrance of Bearcamp Creek, the amount of this plant diminishes as one moves northward. The farthest north *Shortia* was found on this river or its tributaries was in North Carolina, at an elevation of about 1600 feet, between the approach of the Duke Power Road to the river and Windy Falls. In this area C. F. Moore and B. C. Olney found an unusual station, and as Moore describes it, "This interesting location was high on a ridge between the Horsepasture River and Bearwallow Creek, but nearer the Horsepasture. *Shortia* was growing on the dry hillside far removed from any stream. It was not in a cove but on a well exposed crest. There appeared to be several acres of it."[19]

The lower part of Bearcamp Creek and its main north branch were explored well above the North Carolina boundary, and the large quantity of *Shortia* that F. E. Boynton discovered along the lower part of this creek in the fall of 1886 still remains. It was found hanging from the moist wall of the gorges, on decaying fallen trees and in the loose, fertile acid soil (pH 5.2) along the stream. Along Mill Creek, a southern branch of Bearcamp Creek, *Shortia* was frequently found, and in certain places extending up the mountain. As its sources near the divide (circa 1800 ft.), which separates the drainage areas of the Horsepasture River from those of the Thompson River, were reached, *Shortia* became less abundant.

Laurel Fork Creek, the lower main tributary of the Toxaway River above its junction with the Horsepasture River, entends into Pickens County, South Carolina. On this eastern branch, *Shortia* is growing near the lower bridge crossing, about one-fourth mile above its mouth. C. F. Moore and B. C. Olney previously recorded this location. At the old millsite, farther up the creek, it was found in abundance extending up the mountain sides. Numerous stations were observed along the creek and its branches in the two miles explored above the mill-site. In March of this year C. F. Moore and J. L. Kapp found it in

[19] Letter, C. F. Moore to P. A. Davies, June 30, 1952.

abundance further up this creek to an elevation of about 1600 feet.[20] On Jackies Branch, a northern tributary of Laurel Fork Creek, *Shortia* was found near its mouth. No attempt was made to explore the headwaters of this small stream.

Three creeks joining the river just below the North Carolina border were next examined. Cobb and Bear Creek rising in Transylvania County, North Carolina, flow southeast into Oconee County, South Carolina, while the third creek (unnamed) arises in Pickens County, South Carolina, and flows almost due west to the river. Cobb Creek, the smaller and more northerly branch on the west side of the river was explored along the lower two-thirds of its course. This creek had very little water, so conditions were not favorable. A few small patches were found near its mouth. Bear Creek was followed from its confluence with the river to the Duke Power Co. road. Habitats were favorable and many stations of *Shortia* were observed. No examinations were made above the Duke Power Co. road. The eastern unnamed branch was examined but a short distance and several small patches were found.

In the lower part of Transylvania County, three streams enter the Toxaway River at the Cane Brake: Rock and Toxaway Creeks from the east and a small unnamed one from the west. Along the lower and more gentle terrain of Rock (Rockhouse) Creek no *Shortia* was observed. At the narrows about three-fourths mile above its mouth, it was found but not in abundance. No further inspection of this creek was attempted. In 1948 C. F. Moore reported a station higher up near its sources. Toxaway Creek was explored as far as the falls. Again *Shortia* was found along its banks. Frozen Creek, a northern branch of Toxaway Creek, was explored above Frozen Lake without success. The farmers in this area had never seen or heard of it. The unnamed creek from the west was examined about one-half way up its course. Eight stations were counted.

Studies were made on the lower one-fourth mile of Auger Fork Creek. No *Shortia* was found except near the river. The small unnamed creek just above the Auger Fork Creek was examined near the road crossing. No *Shortia* was found at this place.

Bearwallow Creek is a main western division of the Toxaway

[20] Letter C. F. Moore to P. A. Davies Aug. 2, 1954.

River below the falls. With the exception of the Whitewater River area, more persons have observed and collected *Shortia* along the lower part of this creek than in any other part of the Keowee drainage basin. The writer has been along the lower part of this creek five times and has observed patches of *Shortia* each time. The fourth time, the creek was reached from a logging road and trail from F. O. Fisher's place between Rosman and Cashiers on highway 64. No *Shortia* was found along this creek until an elevation of about 1600 feet was reached. The stations along Bearwallow Creek and the one observed on the Toxaway River about one-fourth mile above the entrance of this creek mark the northern station of Shortia observed by the writer in the Keowee drainage area.

The amount of *Shortia* on the drainage areas of the Catawba River is exceedingly small when compared to that on the tributaries of the Keowee River. Except for one small station reported by F. M. Crayton on the Linville River, west Table Rock Mountain in Burke County, all locations are near streams with sources in the lower part of the Bald Mountain chain.

Although several streams, most of which are small and not indicated on available maps, rise from the lower part of the Bald Mountain chain, only three have received names: Toms Creek on the west, Johns Creek (Fish Hatchery Creek) on the southeast, and McGegers Branch to the east. W. C. Coker reports a station on Toms Creek. Milton Bowman and the writer in June 1952 located Coker's station and found one above and another below it. Three small stations were observed on a small unnamed branch of Toms Creek flowing from the southern tip of Bald Mountain. Unfortunately no record was made of the exact location of Hyam's station, although he stated it was on a mountain side near a small stream that flowed into the Catawba River about five miles north of Marion. The area at the southern tip of the Bald Mountain chain fits all known data as to the location of Hyam's station. Here the road from Marion to Turkey and North Coves runs close to the mountain, crossing several streams, and is about five miles north of Marion.

Johns Creek has three main branches, all with sources in the Pisgah National Forest. On the right branch no *Shortia* was

found, probably due to heavy grazing. Along the left branch a small patch was observed on a hillside just above the old sawmill site. Many stations were found on its sources in the national forest. The middle branch, frequently called the fish hatchery branch, has all its sources in the national forest. Above the hatchery and along the main tributary, *Shortia* is growing almost to the top of the ridge.

The stations reported by W. C. Coker on the east side of the Bald Mountain, were checked and found to be in good condition. An examination of McGegers Branch and other streams between it and Johns Creek resulted in several small patches. No explorations were made above McGegers Branch on the east side of the mountains. Limekiln, Cox and Armstrong Creeks on the west side of the Bald Mountain chain were checked at various places without success.

Two attempts were made to reach the Crayton station on the Linville River below the Table Rock Mountains. On April 12, 1952, Milton Bowman and the writer descended the gorge between Hawksbill and Table Rock Mountains. Narrowness of the gorge and high water prevented us from reaching the area directly below Table Rock Mountain although the river was explored for some distance. No *Shortia* was found. Later the river was ascended from Lake James to a place below Chimney Gap before heavy rains forced a retreat. The part examined gave no indication of *Shortia*. A group of senior scouts ascending the river were given leaves and flowers of *Shortia* and instructed where to look. They were particularly asked to search the area directly below Table Rock Mountain. Although their main interest was to ascend the river to the Linville Falls, they did spend some time looking for *Shortia*. Their results were negative. From the writer's experience along this river, he is led to believe that the Crayton station is simply an outpost, and that if other patches are present they are few in number.—

DEPARTMENT OF BIOLOGY, UNIVERSITY OF LOUISVILLE, LOUISVILLE, KENTUCKY.

ECHINODORUS IN THE AMERICAN TROPICS

Norman C. Fassett

(*Continued from p. 188*)

15d. E. TENELLUS, var. **latifolius** (Seubert) Fassett, n. comb. *Alisma tenellum* forma *latifolia* Seubert in Mart. Fl. Bras. **3,** pt. 1: 195, t. 13, fig. 2, nutlet and plant to left. 1848.

Southern Brazil to Venezuela, West Indies, and northern Central America (Map 13d) **Guatemala:** Lake Zotz, Petén, 18 May 1933, *Lundell 3293* (F); Dept. Jalapa, Potrero Carrillo, 13 miles northeast of Jalapa, alt. 1500–1700 m., 12 December 1939, *Steyermark 33098* (F); Dept. Alta Verapaz, bogs near Santa Cruz, along road to San Cristóbal, alt. about 1350 m., 16 April 1941, *Steyermark 42754* (F); Dept. Alta Verapaz, large swamp just east of Yactic, alt. 1300 m., 20 February 1942, *Steyermark 43977* (F). **Honduras:** in bog, in pine forest, El Achote, near Siguatepeque, Dept. of Comayagua, alt. 1500 m., 18 February 1928, *Standley 56099* (US, F). **Jamaica:** growing in swamp, Cornwall, St. Elizabeth, 18 July 1915, *Harriss 12095* (GH, F, MO, NY, US); Cornwall swamp, near Locovia, 1915, *Perkins* (NY). **Dominican Republic:** Prov. de la Vega, prope Tarabacoa in paludosis 550 m. alt., June 1912, *Fuertes 1666* (F, GH, NY, US); Llano Costero, Prov. Sto. Domingo, Cuenca, edge of laguna, 6 January 1929, *Ekman 11025* (US). **Porto Rico:** Laguna Yeguada near Vega Baja, 24 March 1922, *Britton, Britton & Brown 6773* (F, NY, US); muddy marsh, vicinity of San Juan, 11 & 12 February 1914, *Britton & Cowell 1483* (GH, NY, US); Martin Peña, 12 February 1914, *Johnston 1314* (NY). **Venezuela:** Tovar, 1854–55, *Fendler 1358* (GH); La Trinidad de Maracay, at an altitude of 440 meters, State of Aragua, January–February 1913, *Pittier 5844* (NY, US); in morass, El Limón, near Maracay, Aragua, 19 January 1922, *Pittier 10104* (GH, NY, US); Anzoátegui, headwater of Río Guanipa, 28 December 1940, *Pittier 14637* (US). **British Guiana:** herb, on edge of drying pond, basin of Rupununi River, lat. about 2° 52′, 25 & 26 October 1937, *Smith 2285* (F, MO, NY, US). **Bolivia:** Reyes, alt. 1000 ft., October 1921, *Rusby 1540A* (NY, US). **Brazil:** Lagoa Santo, Minas Geraes, 3 August 1936, *Archer 3612* (US); Omolas, Matto Grosso, 6 August 1908, *Hoehne 30* (US). **Paraguay:** in regione lacus Ypacaray, May 1913, *Hassler 12654* (F, GH, MO, US); common in a dry lagoa, Tapytá, April 1931, *Jörgensen 4722* (NY, US, F, MO); fluminis Apa, February 1902, *Hassler 8453* (GH, MO).

This is often the largest phase of *E. tenellus*, some of the plants having a scape 35 cm. long, with leaves 20 cm. long and 12 mm. wide (Fig. 76). A collection from Honduras: El Achote, hills above the plains of Siguatepeque, Dept. Comayagua, *Yuncker, Dawson & Youse 6321* (F), has a slight development of a fourth lateral rib on some achenes. This may represent a

Map 14. Echinodorus isthmicus.

slight introgression from populations to the southeastward in Costa Rica, where that character is well-developed.

E. TENELLUS var. LATIFOLIUS f. **apanecae** Fassett, n.f., plantae in aqua vadosa; foliis linearibus longis-oblanceolatis, 12–22 cm. longis, flaccidis, membranaceis, ad basim attenuatis.—**El Salvador:** in about 1 foot of very cold water, Lagunita las Ninfas, Apaneca, alt. 5430 ft., 28 January 1951, *Fassett 28704* (GH, WIS); shallow water, mud bottom, Laguna Verde, Apaneca, alt. 5100 ft., 28 December 1950, *Fassett 28505* (TYPE in Chicago Natural History Museum, GH); same data, no. *28508* (F); same locality, 30 December 1950, *Fassett 28525* (F).

When the fertile terrestrial form is not found nearby the identification of submersed forms is more difficult. Since *E. tenellus* var. *latifolius* is the only one of this group that has been collected in Central America, these plants presumably belong to

Map 15. Echinodorus magdalenensis, dots; E. quadricostatus, triangle.

that variety. The leaves are much larger than in the terrestrial forms. A few leaves of no. *28508* are a little more like the terrestrial ones, and show the callous margin and tip characteristic of *E. tenellus*.

16. Echinodoras **isthmicus** Fassett, n. sp., foliis lanceolatis, 3–7 cm. longis, 2–5 mm. latis; scapis 6–12 cm. altis, saepi verticillatis; antheris 0.7 mm. longis; achaeniis 1.6 mm. longis, 4-costatis utrinque, rostro nullo aut 0.2 mm. longo (Fig. 69).

Costa Rica and Panama (Map 14). **Costa Rica:** Cienega da Agua Buena, Cañas Gordas, alt. 1100 m., February 1897, *Pittier 11126* (US). **Panama:** wet meadows along Río Caldera, south of El Boquete, alt. 1250 m., 1 March 1918, *Killip 3618* (US—TYPE).

17. Echinodorus **quadricostatus** Fassett, n. sp., laminis foliorum 3.5–5 cm. longis, 3–6 mm. latis; achaeniis 1.8 mm. longis, 4-costulatis utrinque (Fig. 72); rostro 0.8 mm. longo; antheris 0.6 mm. longis.

Northern Peru (Map 15, triangle). **Peru:** Dept. Loreto, Balsapuerto, altitude about 220 meters, January 1933, *Klug 2875* (GH—TYPE; US, F); Dept. Loreto, Yurimaguas, lower Río Huallaga, alt. about 135 meters, 22 August—9 September 1929, *Killip & Smith 27963* (US); lower Río Huallaga, Dept. Loreto, October–November 1929, *Williams 4698* (F).

18. Echinodorus **magdalenensis** Fassett, n. sp., laminis foliorum lanceolatis, 3–5 cm. longis, 5–9 mm. latis; achaeniis 1.6–1.7 mm. longis, costis obscuris aut obsoletis (Fig. 71); rostro 0.6–0.7 mm. longo; antheris 0.4–0.5 mm. longis.

In Colombia, in the basin of Río Magdalena and on the nearby Pacific coast (Map 15, dots). **Colombia:** Department of Antioquia, Puerto Berrio, alt. 130–140 m., 11–13 January 1918, *Pennell 3717* (GH, US), Department of El Valle, Cuchilla, east of Zarzal, alt. 1200–1600 m., 22 July 1922, *Pennell, Killip & Hazen 8523* (US—TYPE); Department of Valle, costa del Pacifico, Isla del Guayabel, en lo desembocadura río Cajambre, 0–5 m. alt., 11 & 12 February 1944, *Cuatrecasas 16229* (US).

IX. Distribution of Characters in Section Tenelli

The morphological relationships as based on nutlets are shown in Figs. 66–72. Specific distinctions are shown by double lines and varietal by single lines; this is on a basis of how the characters act, not on how different they look. The rounded summit of the achene correlates with the beak poorly developed or absent, and plants with 3-ribbed nutlets are quite distinct from those with 4-ribbed nutlets, but the short beak grades imperceptibly into no beak at all and various intermediates are found between the ribbed achenes and the ribless ones. Nine different combinations of characters are theoretically possible, of which 5 have been found.

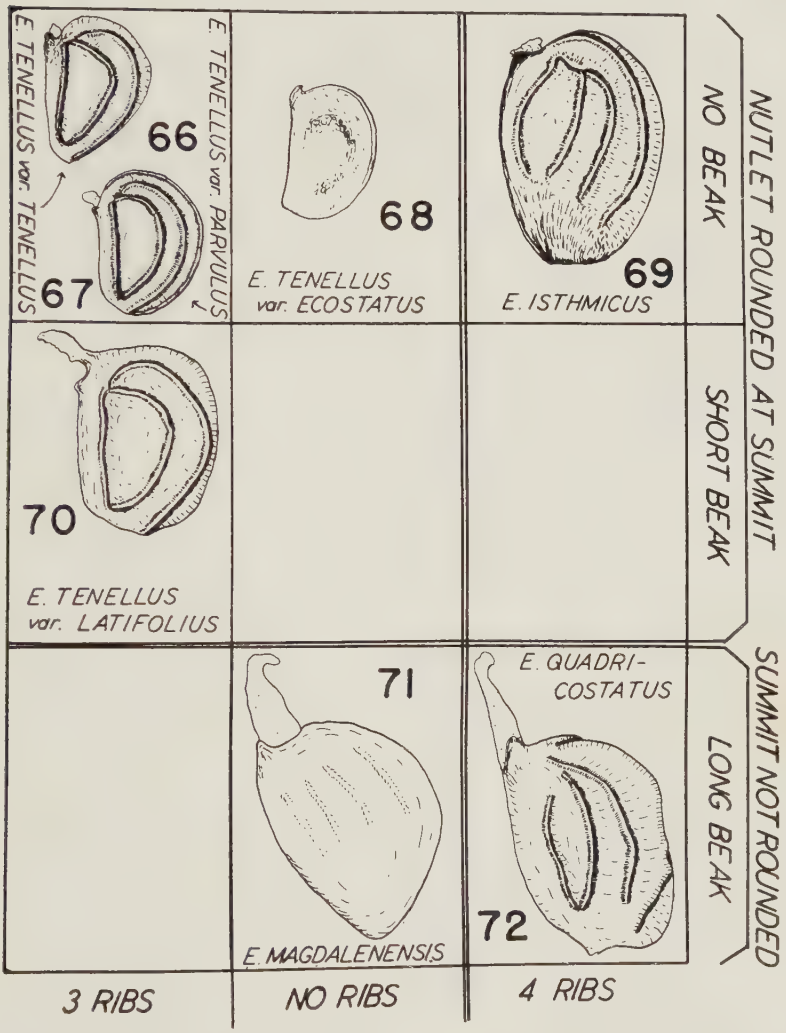


FIG. 66–72. NUTLETS OF SECTION TENELLI (× 20). Fig. 66. *E. tenellus* var. *tenellus*; Brazil, Gardner 2740. Fig. 67. *E. tenellus* var. *parvulus;* Massachusetts, Faxon. Fig. 68. *E. tenellus* var. *ecostatus;* Venezuela, Pittier 11707. Fig. 69. *E. isthmicus;* Panama, Killip 3618. Fig. 70. *E. tenellus* var. *latifolius;* Venezuela, Pittier 5844. Fig. 71. *E. magdalenensis;* Colombia, Pennell 3717. Fig. 72. *E. quadricostatus.* Peru, Killip & Smith 27963. Specimens in United States National Herbarium.

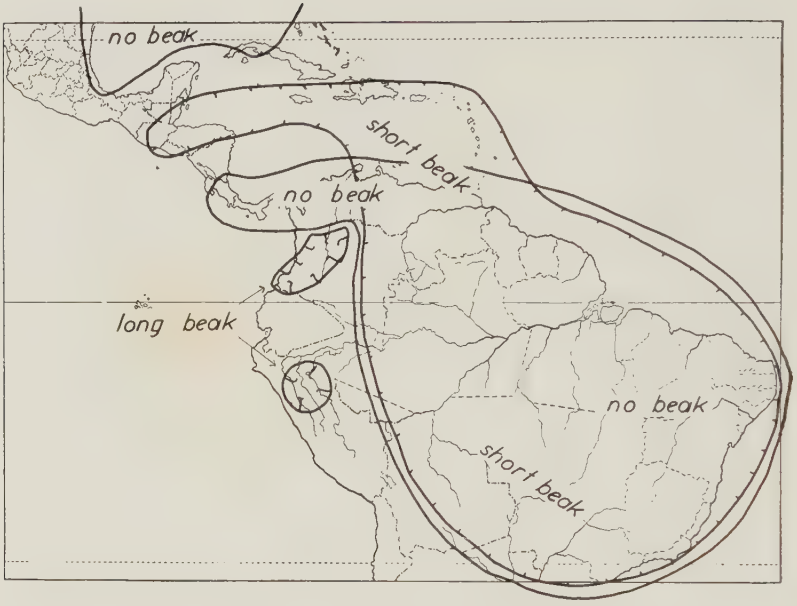
FIG. 73–76. VARIETIES OF E. TENELLUS, NATURAL SIZE, LEAVES OR PLANTS, FROM PHOTOGRAPHIC PRINTS OF SPECIMENS IN US. Fig. 73. Var. *parvulus:* Florida, Harper 39. Fig. 74. Var. *parvulus:* Missouri, Eggert. Fig. 75. Var. *tenellus:* Venezuela, Chardon 252. Fig. 76. Var. *latifolius:* Dominican Republic, Ekman 11025.

On Maps 16 & 17, characters are mapped, and on Map 18 the two previous maps are combined to give a map of the recognized taxa.

Map 16. The long beak, which is correlated with a sloping summit of the nutlet, is in a relatively small area in the northern Andean region. The short beak and undeveloped beak both occur in a great area centering on the Amazon basin, but from this region of coëxistence they reach out in slightly different directions; the short beak follows the geologically ancient route through the Antilles to northern Central America, while the undeveloped beak runs from northern South America into the younger lands of the Isthmus of Panama. The undeveloped beak then reappears in western Cuba and Mexico, ranging thence northward on the Atlantic Coastal Plain to Massachusetts and in the Mississippi embayment to Missouri.

Map 17. The species with 4 ribs on the nutlet have been found in Peru (altitude 135–220 meters) and in Costa Rica and Panama (1199–1250 meters). More widespread is the nutlet with 3 ribs. Lack of ribs is confined to the lowlands from Venezuela and Colombia to Panama; the ribless condition blends on the one hand with the 3-ribbed phase to produce *E. tenellus* var. *ecostatus* (Fig. 68) and combines on the other hand with the 4-ribbed long-beaked *E. quadricostatus* type to produce *E. magdalenensis* (Fig. 71).

From the morphological relationships shown in Figs. 66–72, and the geographical relationships shown in Maps 16–18, we may speculate concerning phylogenetic relationships. Phylogeny is, as is so often the case, more susceptible to speculation than to proof. If we hypothesize as ancestral types *E. tenellus* var. *tenellus* (Fig. 66) mainly of the Amazon basin, and *E. quadricostatus* (Fig. 72) of the headwaters of the Amazon, we may then see *E. tenellus* var. *latifolius* (Fig. 70) as deriving its beak from *E. quadricostatus.* Var. *latifolius* then spreads through the range of var. *tenellus* and beyond it through the Antilles to Central America. As for *E. tenellus* var. *ecostatus* and *E. magdalenensis*, these occupy contiguous areas and are both characterized by partial or complete suppression of ribs; when there is some suggestion of ribs, *E. tenellus* var. *ecostatus* shows 3 and *E. magdalenensis* shows 4. It seems unlikely that



Map 16. Distribution of beak types.

Map 17. Distribution of rib types.

Map 18. Composite of maps 16 and 17 to show distribution of taxa.

the same habit of rib suppression should have originated independently in two species in adjacent areas. The greater constancy of rib suppression in *E. magdalenensis* suggests that that species arose first, perhaps by mutation from an *E. quadricostatus* stock, and that its character has subsequently been transmitted to an *E. tenellus* stock in the geologically young lowlands of Venezuela and adjacent Panama. *E. isthmicus* may be composed of another recombination of the characters of *E. tenellus* and *E. magdalenensis.*

Another hypothesis is suggested by my colleague Dr. Jonathan Sauer, involving *E. magdalenensis* (Fig. 71) as a primitive type, with a genetic make-up involving 4 ribs but with the factor for ribs suppressed; this would involve the origin of *E. quadricostatus* (Fig. 72) from *E. magdalenensis* and an *E. tenellus* stock to introduce expression of the factor for ribs, and of *E. isthmicus* (Fig. 69) and *E. tenellus* var. *ecostatus* (Fig. 68) from different combinations of characters of *E. magdalenensis* and *E. tenellus.*

V. Keys for Identification in Limited Areas

ECHINODORUS IN THE UNITED STATES

a. Slender plants rarely 10 cm. high; carpels 20 or fewer in a loose head; stamens 6 or 9; anthers basifixed; nutlets beakless (Fig. 67).
E. tenellus var. *parvulus.*

a. Robust plants with ovate or cordate leaves (except for dwarfed individuals on drying shores); carpels many in dense heads; stamens 9–30; anthers versatile; nutlets beaked (23–29).

b. Sepals with smooth veins; profile of fruiting head appearing echinate to the naked eye, due to the long (0.5–1.8 mm.) beaks on the nutlets; each side of nutlet with 5 arching ribs of which the 2 wing-like ones are alternate with the others; glands of nutlet acuminate at the upper end and entering the base of the beak (Figs. 25–29); pellucid lines of leaves mostly less than 1 mm. apart and often several mm. long (Fig. 55); scape erect with whorled and usually compound branches.

c. Beak of nutlet 1.2–2.0 mm. long, ½–⅔ as long as the body (Figs. 25–27); anthers 0.8–1.2 mm. long. . . . . *E. Berteroi* var. *Berteroi.*

c. Beak of nutlet 0.5–0.8(–1.0) mm. long, ⅓–½ as long as the body (Figs. 28, 29); anthers 0.5–0.8 mm. long. . *E. Berteroi* var. *lanceolatus.*

b. Sepals with papillose ridges; profile of fruiting heads appearing nearly smooth due to the short (0.2–0.8 mm.) beaks on the nutlets; each side of nutlet with 3–4 abruptly curved and sometimes joining ribs of which the 1 or 2 toward the dorsal edge are wing-like toward the tip (Figs. 23, 24); glands of nutlet rounded at both ends and not closely approaching the beak; pellucid lines of leaves mostly 1 mm. or more apart and rarely exceeding 1 mm. in length (Fig. 54); scape erect when young but soon procumbent, with verticillate peduncles at the nodes. . . . . *E. cordifolius.*

ECHINODORUS IN THE WEST INDIES

a. Carpels 20 or fewer in a loose head; stamens 6–9; anthers basifixed.

b. Leaves narrowly lanceolate or elliptic (Fig. 76); ribs of nutlets not crested (Fig. 70). . . . . *E. tenellus* var. *latifolius.*

b. Leaves cordate; ribs of nutlets crested (Fig. 53). . . . *E. nymphaeifolius.*

a. Carpels many in a dense head; stamens 9–30; anthers versatile.

c. Veins of leaf radiating from base of the blade (Figs. 2, 3, 10); petiole terete or fluted, not 2-winged.

d. Beak more than ½ as long as the body of the nutlet (Figs. 25–27), with tapering apex of glands entering its base; pellucid lines of leaves crowded, often several mm. long (Fig. 55). . . *E. Berteroi* var. *Berteroi.*

d. Beak shorter, the rounded ends of the glands not reaching its base (Figs. 30, 31, 40); leaves with more scattered pellucid short lines (Figs. 57–58) or dots (Fig. 56).

e. Blades with stellate hairs toward the base, about as wide as long (Fig. 10).

f. Blades with pellucid dots and few or no very short lines (Fig. 56), petals white. . . . . *E. grandiflorus* var. *grandiflorus.*

f. Blades with pellucid lines 0.2–0.5 mm. long; flowers yellow.
E. grandiflorus var. *aureus.*

e. Blades glabrous, about twice as long as wide (Fig. 13). . . . *E. ovalis.*

c. Upper pair of veins paralleling the midrib for some distance (Fig. 16); petiole winged. . . . . *E. Grisebachii.*

ECHINODORUS IN MEXICO

a. Carpels 10 or fewer in a loose head; stamens 6–9; anthers basifixed.
  b. Leaves narrowly lanceolate or elliptic (Fig. 73, 74); ribs of nutlet not crested (Fig. 67) ..... *E. tenellus* var. *parvulus.*
  b. Leaves cordate; ribs of nutlet crested (Fig. 53) ..... *E. nymphaeifolius.*
a. Carpels many in a dense head; stamens 9–30; anthers versatile.
  c. Petiole terete or fluted, not winged (Figs. 1–5), blades with clear pellucid dots or lines.
    d. Leaves glabrous, with pellucid lines (Fig. 55).
      e. Nutlets about ⅔ as wide as long, the summit rounded on one side (Fig. 22), with very short beak and round facial glands. . . . *E. virgatus.*
      e. Nutlet twice as long as wide, tapered to the very long beak (Figs. 25–27), the facial glands tapered at apex to enter the base of the beak ..... *E. Berteroi* var. *Berteroi.*
    d. Leaves with stellate hairs and pellucid dots (Fig. 56).
      E. grandiflorus var. *grandiflorus.*
  c. Petiole winged (Figs. 14, 15); blades with very obscure pellucid lines or none ..... *E. Andrieuxi.*

ECHINODORUS IN CENTRAL AMERICA

a. Carpels 20 or fewer in a loose head; stamens 6–9; anthers basifixed.
  b. Leaves narrowly lanceolate or elliptic (Figs. 75, 76); ribs of nutlet not crested (Figs. 68–70).
    c. Facial ribs 3 on each side (Fig. 70), or absent (Fig. 68).
      d. Facial ribs nearly or quite suppressed (Fig. 68); nutlets 0.9–1.1 mm. long; stylar beak absent or nearly so ..... *E. tenellus* var. *ecostatus.*
      d. Facial ribs well developed (Fig. 70); nutlets 1.4–1.8 mm. long; stylar beak 0.2–0.5 mm. long ..... *E. tenellus* var. *latifolius.*
    c. Facial ribs 4 on each side (Fig. 69) ..... *E. isthmicus.*
  b. Leaves cordate; ribs of nutlets crested (Fig. 53) ..... *E. nymphaeifolius.*
a. Carpels many in a dense head; stamens 9–30; anthers versatile.
  e. Sepals 12–20-nerved, thin, withering, not accrescent, reflexed or loosely ascending in fruit, pellucid markings of leaves, if present, not reticulate.
    f. Leaves with blades cordate at base (Figs. 10–12); petioles terete or fluted, not winged; base of blades and summit of petioles with stellate hairs or muricate (Fig. 11).
      g. Flowers pedicelled; blades with few or no pellucid lines, sometimes with pellucid dots.
        h. Blades with copious pellucid dots (Fig. 56)
          E. grandiflorus var. *grandiflorus.*
        h. Blades without pellucid markings ..... *E. muricatus.*
      g. Flowers sessile; blades with very short pellucid lines (Fig. 60).
        E. bracteatus var. *bracteatus.*
    f. Leaves glabrous, with blades tapered (Figs. 14, 16) or subcordate (Fig. 15) at base; petioles 2-winged.
      i. Veins radiating from the base of the blade (Figs. 14, 15); leaves with pellucid lines very obscure or absent; nutlets long-beaked, with 1 facial gland (Figs. 41–43) ..... *E. Andrieuxi.*
      i. Upper pair of veins paralleling the midrib for some distance (Fig. 16); leaves with well-marked pellucid lines (Fig. 63); nutlets short-beaked, with several facial glands (Fig. 51) ..... *E. Grisebachii.*
  e. Sepals about 30-nerved, thick and brittle, enlarging in fruit to cover the fruiting head; pellucid markings reticulate (Fig. 64) ..... *E. tunicatus.*

ECHINODORUS IN TROPICAL SOUTH AMERICA

a. Slender plants rarely 10 cm. high; carpels 20 or fewer in a loose head; stamens 6 or 9; anthers basifixed.

b. Summit of nutlet rounded above the beaklet (Figs. 66, 68, 70); stylar beak 0.5 mm. or less long; facial ribs of nutlet present or absent.

c. Nutlet 0.9–1.1 mm. long; stylar beak nearly absent; anther 0.2–0.6 mm. long.

d. Facial ribs well developed (Fig. 66) ..... *E. tenellus* var. *tenellus.*

d. Facial ribs nearly or quite suppressed (Fig. 68). *E. tenellus* var. *ecostatus.*

c. Nutlet 1.4–1.8 mm. long; stylar beak 0.2–0.5 mm. long (Fig. 70); anther 0.5–1.0 mm. long ..... *E. tenellus* var. *latifolius.*

b. Summit of nutlet horizontal or sloping downward from the beaklet (Fig. 71); stylar beak 0.6–0.7 mm. long; facial ribs of nutlet nearly or quite obsolete ..... *E. magdalenensis.*

a. Robust plants usually 50 cm. or more high; carpels many in dense heads; stamens 9–30; anthers versatile.

e. Leaves with blades more or less cordate at base (Figs. 10–12); petiole terete or fluted but not 2-winged; leaves mostly stellate-pubescent or muricate about summit of petiole and base of blade.

f. Flowers long-pedicelled.

g. Blades with pellucid dots (Fig. 56) .. *E. grandiflorus* var. *grandiflorus.*

g. Blades without pellucid markings.

h. Inflorescence erect, often compound, with pedicels reaching 3 cm. in length ..... *E. muricatus.*

h. Scape creeping, simple, sometimes 2 m. long, rooting at nodes and sometimes proliferous, with erect pedicels sometimes reaching 7 cm. ..... *E. fluitans.*

f. Flowers nearly sessile.

i. Leaves with very short pellucid lines (Fig. 60) and stellate hairs. *E. bracteatus* var. *bracteatus.*

i. Leaves glabrous and without pellucid markings. *E. bracteatus* var. *efenestratus.*

e. Blades tapered (Figs. 18–21) or truncate (Fig. 17) at base; petioles 2-winged.

j. Veins radiating from the base of the blade (Figs. 17–20); internodes of inflorescence sharply keeled but not winged ..... *E. paniculatus.*

j. Upper pair of veins running parallel to the midrib for some distance (Fig. 21); internodes of inflorescence with 3 herbaceous wings about 2 mm. wide ..... *E. trialatus.*

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